7-1-1992

Existence of Traveling-Wave Solutions for a Bistable Evolutionary Ecology Model

Jack D. Dockery

Roger Lui
Worcester Polytechnic Institute, rlui@wpi.edu

SIAM J. MATH. ANAL.
Vol. 23, No. 4, pp. 870–888, July 1992

004

EXISTENCE OF TRAVELLING WAVE SOLUTIONS FOR A BISTABLE EVOLUTIONARY ECOLOGY MODEL*

JACK D. DOCKERY† AND ROGER LUI‡

Abstract. The existence of travelling wave solutions for a density-dependent selection migration model in population genetics is proven. A single locus and two alleles are assumed. It is also assumed that the fitnesses of the heterozygotes in the population are below those of the homozygotes. The method of proof is by constructing an isolating neighborhood and computing a connection index.

Key words. population genetics, travelling waves, wave speed, connection index, isolated invariant set, homotopy

AMS(MOS) subject classifications. 35K57, 92A10

1. Introduction.

During the past two decades, a considerable amount of mathematics has been done on the following nonlinear diffusion equation,

$$u_t = u_{xx} + h(u) \tag{1}$$

where $h \in C^1[0,1], h(0) = 0$ and $h(1) = 0$ [1], [10]. This equation is popular because it has numerous applications, one of which is to describe the dynamics of a certain gene frequency in a population subject to selection pressure and random migration [11]. In such an application, many simplifying assumptions had to be made in order that the situation can be modeled by (1). Some of these assumptions are more serious than others, but the most restrictive is probably the assumption that the population density remains constant throughout space and time. We would like to develop and analyze a model that does not have this requirement, and to compare our results to those of (1). We shall develop such a model in this section. The rest of the paper is devoted to proving the existence of travelling wave solutions for an important case of the model. A complete discussion of selection-migration models and the mathematics of (1) may be found in [9].

Consider a population of diploid individuals living in a one-dimensional homogeneous habitat which we assume to be the entire real line. Suppose a particular pair of chromosomes carries at one of its loci a particular gene that occurs in two forms, called alleles, which we denote by A and a. Then the population may be divided into three classes or genotypes: AA, aa, and Aa. Individuals with the first two genotypes are called homozygotes while individuals with the last genotype are called heterozygotes.

Let $\rho_1(x,t), \rho_2(x,t), \rho_3(x,t)$ be the densities of genotypes AA, Aa, and aa at point x and time t, respectively. We assume that the population mates randomly without regard to genotype, produces offspring at the rate r and that the population diffuses with a constant rate 1. Let τ_1, τ_2, τ_3 denote the death-rates of the individuals with genotypes AA, Aa, and aa, respectively, and let $n(x,t)$ denote the total population

*Received by the editors June 4, 1990; accepted (in revised form) December 2, 1991.

†Department of Mathematical Sciences, Montana State University, Bozeman, Montana, 59715. This research was supported in part by the Institute for Mathematics and Its Applications, University of Minnesota.

‡Department of Mathematical Sciences, Worcester Polytechnic Institute, Worcester, Massachusetts 01609. This research was supported in part by National Science Foundation grant DMS-8920597.

density. Then, under the above assumptions, ρ_1, ρ_2, ρ_3 satisfy the following system of partial differential equations,

$$
\begin{aligned}
\rho_{1,t} &= \rho_{1,xx} - \tau_1\rho_1 + \frac{r}{n}\left(\rho_1 + \frac{1}{2}\rho_2\right)^2, \\
\rho_{2,t} &= \rho_{2,xx} - \tau_2\rho_2 + \frac{2r}{n}\left(\rho_1 + \frac{1}{2}\rho_2\right)\left(\rho_3 + \frac{1}{2}\rho_2\right), \\
\rho_{3,t} &= \rho_{3,xx} - \tau_3\rho_3 + \frac{r}{n}\left(\rho_3 + \frac{1}{2}\rho_2\right)^2.
\end{aligned}
\tag{2}
$$

These equations hold without any assumptions on the dependence of the birth and death rates on x, t and ρ_i.

In population genetics, the frequency of an allele is more interesting than the densities of the genotypes. Let $p(x,t) = (\rho_1 + \frac{1}{2}\rho_2)/n$ be the frequency of allele A in the population. Then a straightforward but tedious calculation yields the following equation for p,

$$
p_t = p_{xx} + 2\frac{p_x n_x}{n} + f(p,n)p(1-p) + \frac{1}{4}\{(\tau_2 - \tau_3)p - (\tau_2 - \tau_1)(1-p)\}\sigma. \tag{3}
$$

In the above equation $f(p,n) = p(\tau_2 - \tau_1) + (1-p)(\tau_3 - \tau_2)$, $\sigma = (\rho_2^2 - 4\rho_1\rho_3)/n^2$, and we have assumed that r and τ_i depend on p and n only. We can also obtain an equation for n by simply adding the equations in (2). Doing so, we obtain,

$$
n_t = n_{xx} + g(p,n)n + (\tau_1 - 2\tau_2 + \tau_3)\frac{\sigma n}{4}, \tag{4}
$$

where $g(p,n) = r - p^2\tau_1 - 2p(1-p)\tau_2 - (1-p)^2\tau_3$. The above method of deriving (3) and (4) from (2) is contained in the appendix of [1].

Equations (3) and (4) are insufficient to determine p and n; we need another equation for σ. The quantity σ measures the deviation of the population from Hardy–Weinberg equilibrium. For discrete-time models, the Hardy–Weinberg principle says that with random mating, and in the absence of factors which affect the gene frequencies, the genotype frequencies will arrive at and remain in the proportion $p^2 : 2p(1-p) : (1-p)^2$ after one generation. Such a proportion is called the Hardy–Weinberg equilibrium. Note that $\sigma = 0$ in this case. In a continuous-time model, Hardy–Weinberg equilibrium is attained only asymptotically [6]. In this paper we shall make the assumption that $\sigma = 0$. Hence we obtain the following reaction-diffusion system,

$$
\begin{aligned}
p_t &= p_{xx} + 2\frac{p_x n_x}{n} + f(p,n)p(1-p), \\
n_t &= n_{xx} + g(p,n)n.
\end{aligned}
\tag{5}
$$

It is worthwhile to see how (1) can be derived from (2) using a scaling argument. Let $v = \rho_2/n$. From (2), an equation for v can be derived which we shall not display here. Let $\epsilon = |\tau_1 - \tau_2| + |\tau_2 - \tau_3|$ and assume that it is sufficiently small. (This is called weak selection in population genetic theory.) Then by rescaling time by ϵ and space by $\sqrt{\epsilon}$, some of the terms in the equation for v will contain an ϵ in front. As a first approximation we set $\epsilon = 0$. Then the terms without ϵ in the equation for v imply that $\sigma = 0$. In other words, Hardy–Weinberg equilibrium is achieved. From (4), under the same scaling of space and time and setting $\epsilon = 0$, we obtain $g(p, n) = 0$. Suppose the birth and death rates are functions of n only. Then since $\tau_1 = \tau_2 = \tau_3 \equiv \tau$, we have $n = K$ which is the root of the equation $r(n) = \tau(n)$. For $\epsilon > 0$, we substitute $\sigma = 0$ and $n = K$ into (3) and obtain (1) where $h(p) = p(1-p)\{p(\tau_2(K) - \tau_1(K)) + (1-p)(\tau_3(K) - \tau_2(K))\}$. The above scaling argument is taken from §2.3 of [9].

By relabeling the two alleles A and a, it can always be assumed that $\tau_3 \geq \tau_1$ so that there are three cases to consider in (1), depending on whether τ_2 lies between, above or below τ_1 and τ_3. These are called the heterozygote intermediate, superior and inferior cases, respectively. In the last two cases, h has an intermediate zero between zero and 1.

The mathematical theory of (1) is very rich and well understood. One of the most intriguing properties is the existence of travelling waves. A travelling wave solution of (1) with speed θ is a nonconstant function $\tilde{u}(z)$ such that $\tilde{u}(x + \theta t)$ satisfies (1) for all x and $t > 0$. For example, in the heterozygote inferior case, if $\int_0^1 h > 0$, then there exists $\theta^* > 0$ such that a monotone travelling wave solution connecting zero to 1 exists if and only if $\theta = \theta^*$.

In this paper, we shall consider the heterozygote inferior case of (5); that is, $\tau_2(n)$ lies above $\tau_i(n)$ for $i = 1, 3$. We prove the existence of travelling wave solutions for (5) under additional assumptions on f and g. We shall discuss these assumptions in the next section. The proof of our existence theorem is based on the connection index from the Conley index theory. For the sake of completeness, we have provided a brief description of this index in §3. The computation of the connection index as well as the proof of our theorem are given in §4. To compute the connection index, we continue the original problem to a problem where the computation is much easier. In the last section, we provide a specific example and show that we can easily follow the above-mentioned continuation method numerically. In a forthcoming paper we shall prove that the travelling wave shown to exist here is stable in the case of weak selection.

2. Hypotheses and result. There are two types of hypotheses for our theorem, those that are motivated by our model ((A1) and (A2) below) and those that are necessary to complete our mathematical argument ((A3) and (A4) below). We begin by listing the hypotheses for f and g.

(A1) f and g are C^1 in p and n with $f_p > 0, f_n > 0, g_n < 0$ for $0 \leq p \leq 1$ and $n \geq 0$. Also, the relation

$$g_p(p, n) = f(p, n) \tag{6}$$

holds.

(A2) The nullclines $f = 0$ and $g = 0$ intersect at a point (p^*, n^*) in the region

$$Q \equiv \{(p, n) | 0 < p < 1 \text{ and } n > 0\} \quad \text{with } p^* < \tfrac{1}{2}.$$

(A3) Let the curve $g = 0$ intersect the line $p = 0$ at K_3 and the line $p = 1$ at K_1. We assume that $0 < K_3 < K_1$ and

$$\int_0^{p^*} f(p, K_3)p(1-p)dp < 0.$$

(A4) There exists $\alpha > 0$ such that $f(p, n^*) \geq \alpha(p - p^*)$ for $0 \leq p \leq 1$ and

$$g(0, n^*) < \frac{\min(1, \alpha)}{2}\left(\frac{1}{2} - p^*\right)^2. \tag{7}$$

From (A1) and (A2), one can determine the form of the nullclines $f(p, n) = g(p, n) = 0$. They are shown in Fig. 1.

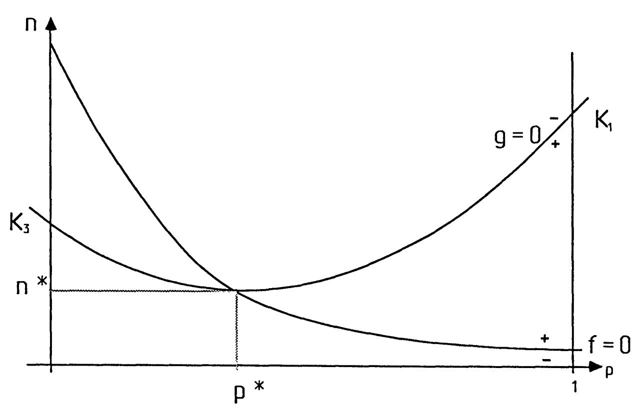

FIG. 1. *The form of the nullclines $f = 0$ and $g = 0$.*

We now explain how hypotheses (A1) and (A2) can be satisfied by our model.

Suppose the functions r and $\tau_i, i = 1, 2, 3$ depend only on n (density-dependent selection) and that they are continuously differentiable on the interval $[0, \infty)$. It is more convenient to write f and g in terms of the fitness functions η_i where $\eta_i(n) = r(n) - \tau_i(n)$. Doing so, we obtain,

$$\begin{aligned} f(p, n) &= p(\eta_1 - \eta_2) + (1-p)(\eta_2 - \eta_3), \\ g(p, n) &= p^2\eta_1 + 2p(1-p)\eta_2 + (1-p)^2\eta_3. \end{aligned} \tag{8}$$

Condition (6) is therefore satisfied. The function g represents the fitness of the entire population.

We are interested in the heterozygote inferior case of (5). A weaker condition than heterozygote inferiority is $\eta_1 + \eta_3 > 2\eta_2$ for $n \geq 0$. From (8), this is equivalent to the condition $f_p > 0$ for $n \geq 0$ in (A1).

In ecological models, it is frequently assumed that resources are scarce so that the growth rate of the population decreases with increase in population size. Thus, it is reasonable to assume that η_i is a decreasing function of n, positive near zero and negative for large n. This implies that $g_n < 0$ and that for each p, $g(p,n) = 0$ has a (unique) positive root.

Finally, from (8), the condition $f_n > 0$ for $0 \leq p \leq 1$ and $n \geq 0$ in (A1) is equivalent to $\eta_1^{'} > \eta_2^{'} > \eta_3^{'}$. Such an assumption is important because it allows us to use the comparison principle on the first equation of (5). The comparison principle is not valid for (5). For an example where these inequalities and $\eta_1 + \eta_3 > 2\eta_2$ are satisfied let $\eta_i(n) = r_i(1-(n/K_i)), i = 1,2,3$ where r_i, K_i are positive constants chosen so that $2r_2 < r_1+r_3$, $r_1/K_1+r_3/K_3 < 2(r_2/K_2)$ and $r_1/K_1 < r_2/K_2 < r_3/K_3$.

Since $f_p > 0$ and $g_n < 0$, the implicit function theorem implies that there exist functions $\tilde{n}$ and $\hat{n}$ such that $f(p,\tilde{n}(p)) = 0$ and $g(p,\hat{n}(p)) = 0$ for p in the unit interval. Since $f_n > 0$, $\tilde{n}$ is decreasing in p. We assume that the graphs of $\tilde{n}$ and $\hat{n}$ intersect at some point (p^*, n^*) where $0 < p^* < \frac{1}{2}$ and $n^* > 0$. From (6), it is easy to see that (p^*, n^*) is unique and $\hat{n}$ achieves a minimum at p^*. From (8), the function f can be written as $f(p,n) = C_1(n)(p - C_2(n))$, where $C_1(n) = \eta_1 + \eta_3 - 2\eta_2$ and $C_2(n) = (\eta_3 - \eta_2)/(\eta_1 + \eta_3 - 2\eta_2)$. Thus $p^* < \frac{1}{2}$ if and only if $\eta_3(n^*) < \eta_1(n^*)$.

Hypotheses (A1) and (A2) are not enough to prove our theorem. Two technical assumptions, (A3) and (A4), have to be added. Assumption (A3) is used only in the proof of Lemma 4.4 while (A4) is used only in the proof of Lemma 4.9. Recall the definition of $C_2(n)$ from the above paragraph. From the form of f given above, we see that the condition $f(p,n^*) \geq \alpha(p-p^*)$ is an equality and is always satisfied. Also, (7) is satisfied for sufficiently small p^* since $g(0,n^*) = \alpha(p^*)^2$. To see this, solve p^* in terms of $\eta_i(n^*)$ by writing $g(p^*, n^*) = 0$ as a quadratic equation in p^*. From the above paragraph, $p^* = C_2(n^*)$. Setting these two quantities equal, we obtain $\eta_2^2(n^*) = \eta_1(n^*)\eta_3(n^*)$ which is equivalent to $g(0,n^*) = \alpha(p^*)^2$. Finally, substituting $\eta_2(n^*) = -\sqrt{\eta_1(n^*)\eta_3(n^*)}$ into $p^* = C_2(n^*)$, we obtain

$$p^* = \frac{\sqrt{\eta_3(n^*)}}{\sqrt{\eta_1(n^*)} + \sqrt{\eta_3(n^*)}}$$

so that p^* is small if and only if $\eta_3(n^*)/\eta_1(n^*)$ is small.

It is obvious that the constant solutions of (5) in $\mathrm{cl}(Q)$ are $(0,0)$, $(1,0)$, (p^*, n^*), $(0, K_3)$ and $(1, K_1)$. If we only consider solutions that are spatially homogeneous, then (5) becomes a system of ordinary differential equations. From assumption (A1), it is easily checked that the first three solutions are unstable and the last two are stable. This type of system where there are exactly two stable equilibria is better known as a bistable system.

By a travelling wave solution of (5) with speed θ, we mean a nonconstant, bounded solution $(\tilde{p}, \tilde{n})$ such that $(\tilde{p}, \tilde{n})(x + \theta t)$ satisfies (5) for all x and $t > 0$. Equivalently, $(\tilde{p}, \tilde{n})$ satisfies the system of ordinary differential equations,

$$\begin{aligned} p'' - \theta p' + 2\frac{p'n'}{n} + f(p,n)p(1-p) &= 0, \\ n'' - \theta n' + g(p,n)n &= 0, \end{aligned} \tag{9}$$

on $\mathbf{R}$ where $' = d/dz$. As in the case of a single equation, we look for a travelling wave solution of (5) which connects the two stable equilibria $(0, K_3)$ and $(1, K_1)$; i.e., $(\tilde{p}, \tilde{n})$ satisfies the boundary conditions:

$$\lim_{z\to-\infty}(p(z),n(z)) = (0,K_3),$$
$$\lim_{z\to\infty}(p(z),n(z)) = (1,K_1). \tag{10}$$

Under the hypotheses (A1)–(A4) we can prove the following theorem.

THEOREM 2.1. *There exists a positive wave speed θ such that* (9) *has a solution* $(\tilde{p},\tilde{n})$ *which satisfies* (10). *Furthermore, $\tilde{p}' > 0$ while $\tilde{n}$ has at most one local minimum on* $\mathbf{R}$.

The proof of Theorem 2.1 is based on the connection index theory.

3. The connection index. In this section we shall provide a cursory description of the connection index so that readers who are unfamiliar with such concepts can understand the proof of our theorem quickly. Many technical details are therefore omitted, but they can all be found in the papers [4], [5], [12]. The connection index is actually based on the Conley index [3] which we now describe.

3.1. The Conley index. Consider a flow defined by an autonomous system of differential equations on $\mathbf{R}^n$. Suppose $N \subset \mathbf{R}^n$ is compact. Let $I(N)$ denote the set of all points $x \in \mathbf{R}^n$ whose entire orbit (solution curve) through x is contained in N. If $S = I(N)$ is interior to N, then S is an isolated invariant set and N an isolating neighborhood. It is clear that a compact set N is an isolating neighborhood for S if every orbit which hits the boundary of N eventually leaves N in either forward or backward time, and if no orbit in S gets arbitrarily close to the boundary of N.

DEFINITION 1. Let S be an isolated invariant set with isolating neighborhood N. An *index pair* for S is a pair of compact sets (N_1, N_0) with $N_0 \subset N_1 \subset N$ such that:

(i) $\mathrm{cl}(N_1 \backslash N_0)$ is an isolating neighborhood for S.

(ii) N_i is positively invariant relative to N for $i=0,1$, i.e., given $x \in N_i$ and $x \cdot [0,t] \subset N$, then $x \cdot [0,t] \subset N_i$.

(iii) N_0 is an exit set for N_1, i.e., if $x \in N_1$, $x \cdot [0,\infty) \not\subset N_1$, then there is a $T \geq 0$ such that $x \cdot [0,T] \subset N_1$ and $x \cdot T \in N_0$.

Given an index pair, the Conley (homotopy) index of S is defined to be the homotopy type of the pointed space N_1/N_0 obtained by collapsing N_0 to a point. This homotopy index is well defined and depends only on the invariant set S [3]. We shall denote the Conley index of S by $h(S)$.

The easiest example is when $S = \emptyset$. Then $(\emptyset, \emptyset)$ is an index pair. On collapsing the empty set to a point, a pointed one-point space is obtained. The homotopy type of this space, hence $h(\emptyset)$, is denoted by $\overline{0}$. If S is a hyperbolic rest point for the flow with a k-dimensional unstable manifold, then $h(S) = \Sigma^k$, the homotopy type of a pointed k-sphere.

An important property of the index is the sum formula. The sum of two pointed spaces (A,a) and (B,b) is defined as $A \cup B/\{a,b\}$, the pointed space obtained by taking the union of A and B and identifying the distinguished points a and b. This sum is denoted by $(A,a) \vee (B,b)$. If S_1 and S_2 are two isolated invariant sets with $S_1 \cap S_2 = \emptyset$, then $h(S_1 \cup S_2) = h(S_1) \vee h(S_2)$. Furthermore, $\overline{0} \vee h(S) = h(S)$ for any isolated invariant set S.

The product of two pointed spaces can also be defined. If S_1 and S_2 are isolated invariant sets for the two flows $x' = f(x)$ and $y' = g(y)$, respectively, then $S_1 \times S_2$

is an isolated invariant set for the product flow. The index of $S_1 \times S_2$ is given by $h(S_1 \times S_2) = h(S_1) \wedge h(S_2)$ where $\wedge$ is the smash product. For pointed spheres, we have $\Sigma^m \wedge \Sigma^n = \Sigma^{m+n}$ for all m and $n \geq 0$. Furthermore, $\overline{0} \wedge h(S) = \overline{0}$.

Finally, the Conley index also has the continuation property. Suppose S is an isolated invariant set with isolating neighborhood N and we continuously deform the flow so that N remains an isolating neighborhood throughout. Then the index of S before and after the deformation are the same.

3.2. The connection index. Suppose that a one-parameter family of flows on $\mathbf{R}^n$ is given by

$$x' = f(x, \theta) \tag{11}$$

where f depends continuously on $\theta \in [\theta_1, \theta_2]$. By appending the equation

$$\theta' = 0, \tag{12}$$

we obtain a flow, denoted by Φ, on $X = \mathbf{R}^n \times [\theta_1, \theta_2]$. Let S, S', and S'' be isolated invariant sets for the flow Φ and let $S(\theta)$ denote the θ slice of S.

DEFINITION 2. The triple (S, S', S'') is called a connection triple if:

(i) $S' \cup S'' \subset S$,

(ii) $S' \cap S'' = \emptyset$,

(iii) $S(\theta) = S'(\theta) \cup S''(\theta)$ for $\theta = \theta_1$ and θ_2.

A homotopy invariant index, called the connection index, can be defined for the connection triples [5]. It has many properties similar to the Conley index. We denote the connection index by $\overline{h}(S, S', S'')$ and postpone its definition together with an example to the end of this section.

Our proof of Theorem 2.1 relies on the following result in [5].

THEOREM 3.1. *Let (S, S', S'') be a connection triple for the flow Φ and suppose that $S = S' \cup S''$. Then $\overline{h}(S, S', S'') = (\Sigma^1 \wedge h(S')) \vee h(S'')$, where $h(S')$ and $h(S'')$ are the Conley indices of S' and S'' for the flow Φ, respectively.*

This theorem clearly implies that if one can prove that $\overline{h} \neq (\Sigma^1 \wedge h(S')) \vee h(S'')$ for some connection triple (S, S', S''), then there exists $\theta \in (\theta_1, \theta_2)$ such that $S(\theta) \not\subset S'(\theta) \cup S''(\theta)$. Our connection triple is constructed so that $S'(\theta)$ and $S''(\theta)$ are the rest points. Therefore there must be another orbit in $N(\theta)$ besides $S'(\theta)$ and $S''(\theta)$. From our construction of the isolating neighborhood, this orbit in $N(\theta)$ is the desired travelling wave with wave speed θ.

To show that $\overline{h} \neq (\Sigma^1 \wedge h(S')) \vee h(S'')$, we compute $\overline{h}$, $h(S')$ and $h(S'')$ via a continuation argument. The idea is similar to that of the Conley index described at the end of the previous section. We parameterize the flow Φ on X by $\lambda \in [0,1]$ and call it $\Phi(\lambda)$ where $\Phi(1) = \Phi$. Let $Y = X \times [0,1]$ with the obvious flow defined on Y and let S_0 and S_1 be isolated invariant sets for the flows $\Phi(0)$ and $\Phi(1)$, respectively. Then S_0 and S_1 are said to be related by continuation if there is an isolating neighborhood N for the flow on Y such that $S_0 = I(N(0))$ and $S_1 = I(N(1))$. ($N(\lambda)$ is the λ slice of N and is an isolating neighborhood for $\Phi(\lambda)$.) According to §3.1, $h(S_0) = h(S_1)$. Presumably, $h(S_0)$ is easier to compute than $h(S_1)$. Similarly, we can define a continuation of connection triples. Suppose S', S'', S''' are isolated invariant sets for the flow on Y such that for each λ, $(S'(\lambda), S''(\lambda), S'''(\lambda))$ is a connection triple. Then the connection triples at $\lambda = 0$ and at $\lambda = 1$ are related by continuation and have the same connection index.

We now give the definition of a connection triple (S, S', S''). The following is taken from [5].

Extend the flow (11) so that it is defined for $\theta \in [\theta_1 - \epsilon, \theta_2 + \epsilon]$ for some $\epsilon > 0$. Let U' and U'' be open neighborhoods in $\mathbf{R}^n \times [\theta_1 - \epsilon, \theta_2 + \epsilon]$ of $S'(\theta_1) \cup S'(\theta_2)$ and $S''(\theta_1) \cup S''(\theta_2)$, respectively, and choose them so that they have disjoint closures. Let ϕ be a continuous real-valued function on $\mathbf{R}^n$ which is positive on U' and negative on U'' and zero everywhere else. Append to the above given family of equations the equation $\theta' = \mu\phi(x)[\theta - (\theta_1 + \theta_2)/2]$, where μ is a small positive parameter. Let N be a compact neighborhood in $\mathbf{R}^n \times (\theta_1 - \epsilon, \theta_2 + \epsilon)$ such that $N(\theta)$ is an isolating neighborhood of $S(\theta)$ for each θ. Then there is a $\mu_0 > 0$ such that if $\mu \in (0, \mu_0)$, then N is an isolating neighborhood for the appended equation. Let h_μ be the Conley index of $I(N)$ for $\mu \in (0, \mu_0)$. Then h_μ is independent of μ and in fact depends only on the triple (S, S', S''). We define $\overline{h}(S, S', S'') = h_\mu$.

By way of example, consider the following system of equations,

$$
\begin{aligned}
u' &= v, \\
v' &= \theta v - u(1-u)(u-u^*)
\end{aligned}
$$

where $\theta > 0$ and $u^* \in \frac{1}{2}$. This is the bistable equation which has an increasing travelling wave solution connecting $(u, v) = (0, 0)$ to $(1, 0)$ for a positive wave speed $\theta = \theta^*$. The points $(0, 0)$ and $(1, 0)$ are saddles for all values of θ while $(u^*, 0)$ changes from an unstable spiral to an unstable node as θ increases, say from θ_1 near zero to $\theta_2 > \theta^*$. The phase plane diagram for the two values of θ are shown in Fig. 2 and 3 below. An isolating neighborhood is also shown where the exit set is marked. Let N denote this set cross $[\theta_1, \theta_2]$. Then N is an isolating neighborhood for the above flow and $\theta' = 0$. Let $S = I(N)$, $S' = (0, 0) \times [\theta_1, \theta_2]$, and $S'' = (1, 0) \times [\theta_1, \theta_2]$. Then (S, S', S'') is a connection triple according to Definition 2. To calculate its index, one can follow the recipe described in the above paragraph. An easier, though somewhat incorrect, method is the following (see §4B of [12]).

Let N_0 be a subset of N such that $(N(\theta), N_0(\theta))$ forms an index pair for $S(\theta)$. N_0 is just the exit set of N. Let $\hat{N}_0$ be N_0 together with the closure of all orbit segments in $N(\theta_1)$ and $N(\theta_2)$ which tend to $S'(\theta_1)$ and $S'(\theta_2)$ in negative time, respectively. Then $\overline{h}(S, S', S'')$ is the homotopy type of the pointed space $N/\hat{N}_0$. The reason why this is somewhat incorrect is because $S'(\theta_i) \not\subset N \backslash \hat{N}_0$, $i = 1, 2$, so that $(N, \hat{N}_0)$ is technically not an index pair according to the definition in the previous section. Therefore, we have to modify the flow near $S'(\theta_i)$ and $S''(\theta_i)$,$i = 1, 2$. It turns out that the homotopy type of N/N_0 for the modified flow is the same as the homotopy type of $N/\hat{N}_0$ as defined above.

Now the exit set at θ_i, $i = 1, 2$, consists of three disjoint parts and two of these parts are connected to the unstable manifold at $S'(\theta_i)$. (See Figs. 2 and 3.) Therefore, $\hat{N}_0$ is contractable to a point on the boundary of N, which is homotopic to the surface of a ball. Thus $N/\hat{N}_0$ is homotopy equivalent to the one-point space, or $\overline{0}$. The connection index is $\overline{0}$ for this example.

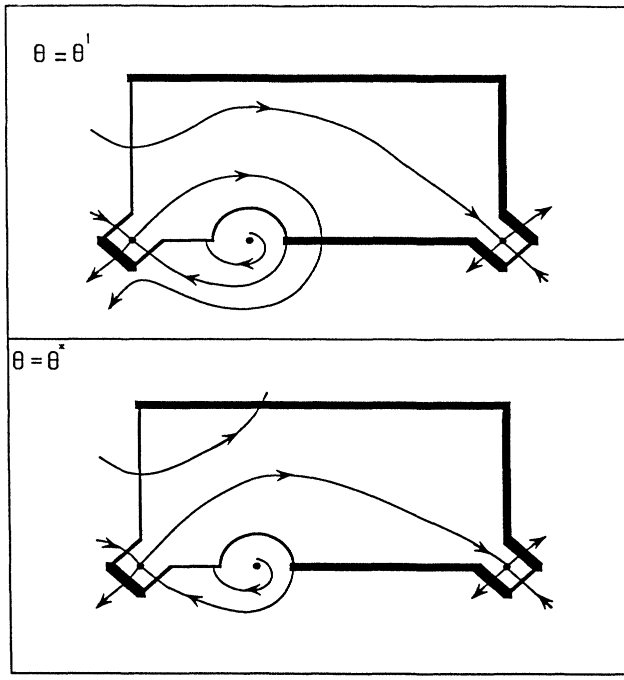

FIG. 2. *The phase planes for the bistable equation at $\theta = \theta_1$ and θ^*.*

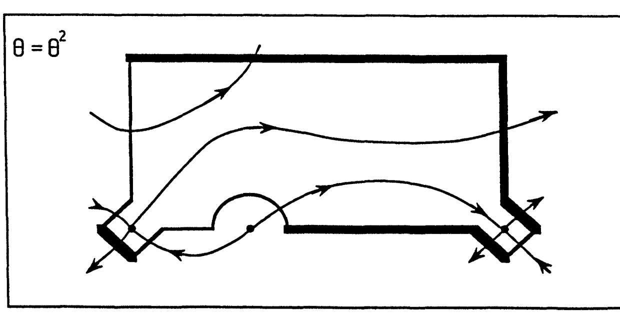

FIG. 3. *The phase plane for the bistable equation at $\theta = \theta_2$.*

4. Proof of Theorem 2.1. In this section we shall use the connection index to prove the existence of travelling waves. It is difficult to compute this index for the original model, so we continue the model to a system for which the connection index is easy to compute and then apply the continuation theorem in the previous section.

4.1. The homotopy. Let $\lambda \in [0,1]$ and consider the system,

$$(13)\qquad \begin{aligned} p'' - \theta p' + 2\lambda\frac{p'n'}{n} + f^\lambda(p,n)p(1-p) &= 0, \\ n'' - \theta n' + g^\lambda(p,n)n &= 0, \end{aligned}$$

where $f^\lambda(p,n) = \lambda f(p,n) + (1-\lambda)(p-p^*)$ and $g^\lambda(p,n) = \lambda g(p,n) + (1-\lambda)(n^*-n)$. When $\lambda = 1$, we recover our original model and when $\lambda = 0$, (13) decouples into the

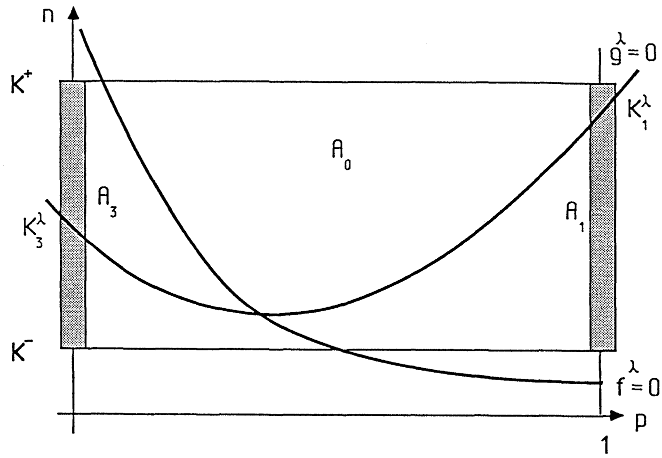

FIG. 4. *Projection of the isolating neighborhood onto the p-n plane.*

bistable equation,

$$p'' - \theta p' + p(1-p)(p-p^*) = 0 \tag{14}$$

and the Fisher equation,

$$n'' - \theta n' + n(n^* - n) = 0. \tag{15}$$

It is easy to check that except for (6), conditions (A1) to (A3) of §2 hold for f^λ and g^λ with K_i replaced by K_i^λ, $i = 1, 3$. We define K_i^λ by $g^\lambda(0, K_3^\lambda) = 0$ and $g^\lambda(1, K_1^\lambda) = 0$. The nullclines $f^\lambda = 0$ and $g^\lambda = 0$ are similar in form to the nullclines $f = 0$ and $g = 0$, respectively. In fact, $f^\lambda = 0$ lies between $f = 0$ and $p = p^*$ while $g^\lambda = 0$ lies between $g = 0$ and $n = n^*$. They intersect only at (p^*, n^*).

It is convenient to write (13) as a first order system:

$$\begin{aligned} p' &= v_1, \\ v_1' &= \theta v_1 - 2\lambda\frac{v_1 v_2}{n} - f^\lambda(p,n)p(1-p), \\ n' &= v_2, \\ v_2' &= \theta v_2 - g^\lambda(p,n)n. \end{aligned} \tag{16}$$

For each θ and λ, (16) defines a flow on $\mathbf{R}^4$. The rest points are $Y_1^\lambda = (1, 0, K_1^\lambda, 0)$, $Y^* = (p^*, 0, n^*, 0)$, $Y_3^\lambda = (0, 0, K_3^\lambda, 0)$, $(1,0,0,0)$ and $(0,0,0,0)$. A travelling wave solution of (5) corresponds to a solution of (16) which connects Y_3^1 to Y_1^1.

4.2. The isolating neighborhood. We first find a set N in $\mathbf{R}^4$, independent of θ and λ, such that it is an isolating neighborhood for the flow (16). The only rest points in N are Y_1^λ and Y_3^λ, and p is increasing along any nonconstant orbit in N.

Let K^+ and K^- be such that $0 < K^- < K_1^\lambda, K_3^\lambda < K^+$ for all $\lambda \in [0,1]$, $f = 0$ intersects $p = 0$ above K^+ and intersects $p = 1$ below K^-. Let $A_0 = \{(p,n) \mid 0 \leq p \leq 1 \text{ and } K^- \leq n \leq K^+\}$ (see Fig. 4).

If $Y = (p, v_1, n, v_2)$ is a solution of (16) with $\theta \geq \theta_0 > 0$ and $-1 \leq p(z) \leq 2$, $K^- \leq n(z) \leq K^+$ for all $z \in \mathbf{R}$, then $|v_i| \leq L$ for $i = 1, 2$. To see this, choose C such that $|g^\lambda(p,n)n| \le C$ for all $\lambda \in [0,1]$ and above values of p, n and define $L = C/\theta_0$. Suppose $v_2(z_0) > L$. Then from (16), $v_2'(z_0) > 0$ which implies that $v_2(z) > L$ for all $z \ge z_0$. Hence n is unbounded which is a contradiction. Thus, $|v_2| \le L$. A similar argument can be used to show that $|n^{2\lambda}p'|$, and hence $|p'|$, is bounded if we observe that p satisfies the equation,

$$(n^{2\lambda}p')' - \theta(n^{2\lambda}p') + f^\lambda(p,n)p(1-p)n^{2\lambda} = 0.$$

Let $N_0 = \{(p, v_1, n, v_2) | (p,n) \in A_0, 0 \le v_1 \le L \text{ and } |v_2| \le L\}$. N_0 is not an isolating neighborhood since Y_1^λ, Y_3^λ and Y^* belong to the boundary of N_0. We need to add to N_0 neighborhoods of Y_1^λ and Y_3^λ and remove a neighborhood of Y^* to obtain an isolating neighborhood.

To add a neighborhood of Y_3^λ, let $A_3 = \{(p,n) \mid |p| \le \delta, K^- \le n \le K^+\}$ where δ is independent of λ. By assumption (A1) we can choose $\delta > 0$ small enough so that $g^\lambda = 0$ intersects the boundary of A_3 only in the $|p| = \delta$ faces for all $\lambda \in [0,1]$ and A_3 lies below the curve $f = 0$ (see Fig. 4). Let $N_3 = \{(p, v_1, n, v_2) \mid (p,n) \in A_3 \text{ and } |v_i| \le L \text{ for } i = 1,2\}$. Recall that $I(N)$ is the set of all orbits of (16) that lie in N for all z.

LEMMA 4.1. $I(N_0 \cup N_3) = I(N_0)$.

Proof. We need to show that $p \ge 0$ and $v_1 \ge 0$ along any orbit in $I(N_0 \cup N_3)$ so that the orbit actually lies in $I(N_0)$.

Let $Y = (p, v_1, n, v_2)$ be an orbit in $I(N_0 \cup N_3)$. Suppose p has a negative minimum at z_0 where $v_1(z_0) = 0$ and $v_1'(z_0) \ge 0$. Since $f^\lambda(p,n) < 0$ if $p < 0$ and $n \in [K^-, K^+]$, (16) implies that $v_1'(z_0) < 0$ which is a contradiction. Therefore, $p \ge 0$.

Now suppose $v_1(z_0) < 0$. If $v_1(z) < 0$ for all $z < z_0$, then Y must tend to a rest point in N_3 as $z \to -\infty$. There is only one rest point in N_3, namely Y_3^λ. Since $p \ge 0$, we must have $p(-\infty) > p(0) \ge 0$ which contradicts the fact that $p = 0$ at Y_3^λ. Therefore, $v_1(z_1) = 0$ for some $z_1 < z_0$ and $v_1(z) < 0$ on $(z_1, z_0]$. Hence $v_1'(z_1) \le 0$. This assumption also implies that $(p,n)(z) \in A_3$ for all $z \in [z_1, z_0]$ and hence $f^\lambda(p,n) < 0$ at $z = z_1$. From (16), $v_1'(z_1) \ge 0$ and hence $v_1'(z_1) = 0$ and $p(z_1) = 0$. But then Y must lie in the invariant manifold $p \equiv 0$, $v_1 \equiv 0$ because of uniqueness which then contradicts the assumption that $v_1(z_0) < 0$. Therefore, $v_1 \ge 0$. This completes the proof of the lemma. □

We add a neighborhood of Y_1^λ in a similar manner. Let $A_1 = \{(p,n) \mid |p-1| < \delta_1, K^- \le n \le K^+\}$. We choose δ_1 independent of λ and sufficiently small so that $g^\lambda = 0$ intersects the boundary of A_1 only in the $p = 1 - \delta_1$ and $p = 1 + \delta_1$ faces (see Fig. 4). Let $N_1 = \{(p, v_1, n, v_2) \mid (p,n) \in A_1 \text{ and } |v_i| \le L \; for \; i = 1,2\}$. The proof of the following lemma is similar to that of Lemma 4.1 and is omitted.

LEMMA 4.2. $I(N_0 \cup N_1 \cup N_3) = I(N_0)$.

Let $\hat{N} = N_0 \cup N_1 \cup N_3$. $\hat{N}$ is still not an isolating neighborhood since Y^* is on its boundary. We need to remove a neighborhood of Y^*. To do this we first show that $v_1 > 0$ along any nonconstant orbit in $I(\hat{N})$.

LEMMA 4.3. *For any orbit $Y \in I(\hat{N})$, $n \ge n^*$ for all $z \in \mathbf{R}$.*

Proof. Suppose n has a local minimum less than n^* at say $z = 0$. Then $(p,n)(0)$ must lie in the region where $g^\lambda > 0$. From (16), $v_2'(0) < 0$ which is a contradiction. Therefore $n \ge n^*$ for all z. □

LEMMA 4.4. *Let $\theta > 0$. Then $v_1 > 0$ along any orbit in $I(\hat{N})$ except when the orbit is Y^*, Y_3^λ, or Y_1^λ.*

Proof. Suppose Y is an orbit in $I(\hat{N}) = I(N_0)$ with $v_1(z) = 0$ at say $z = 0$. Then $v_1'(0) = 0$ for otherwise Y would leave N_0 in either forward or backward time. From (16), $f^\lambda(p,n)p(1-p) = 0$ at $z = 0$. If $p(0) = 0$ or 1, then Y lies in the invariant manifold $p \equiv 0, v_1 \equiv 0$ or $p \equiv 1, v_1 \equiv 0$. In each case, a simple phase plane analysis reveals that the only orbit that lies between K^+ and K^- for all z is the rest point Y_3^λ or Y_1^λ, respectively. Thus we need only consider the case $f^\lambda(p(0), n(0)) = 0$. From Lemma 4.3, the point $(p(0), n(0))$ must lie on or above the curve $g^\lambda = 0$ which implies that $p(0) \leq p^*$. If it lies on $g^\lambda = 0$ and $v_2(0) = 0$, then $Y \equiv Y^*$. Otherwise, Y must tend to Y_3^λ as $z \to -\infty$. To see this, differentiate the equation for p to obtain $p''' + [f(p,n)]'p(1-p) = 0$ at $z = 0$. Since $p'''(0) \geq 0$, we have $n'(0) \leq 0$. If $n'(0) = 0$, then (16) implies that n has a local minimum at $z = 0$. Otherwise, $n'(0) < 0$. In both cases, since n cannot have a local maximum at a point above $g^\lambda = 0$ or a local minimum below it, we conclude that $(p,n)(-\infty) = (0, K_3^\lambda)$ and that $n' \leq 0$ for $z < 0$.

Multiply the first equation in (13) by $p' = v_1$ and integrate to obtain:

$$(17) \qquad \theta \int_{-\infty}^{0} (p')^2 dz = \int_0^{p(0)} f^\lambda(p, n(z^{-1}(p)))p(1-p)dp + 2\lambda \int_{-\infty}^{0} \frac{n'(p')^2}{n} dz.$$

The right side of (17) is less than $\int_0^{p^*} f^\lambda(p, K_3^\lambda)p(1-p)dp < 0$ because $n' < 0$ for $z < 0$, $f_n > 0$ and assumption (A3). This contradicts the assumption that $\theta > 0$. Therefore $v_1 > 0$ along any nonconstant orbit in $I(\hat{N})$. □

It now follows that the only orbit of (16) in $I(\hat{N})$ that hits the boundary of $\hat{N}$ is the constant solution Y^*. To see this, we may assume that the orbit Y lies entirely in N_0 because of Lemma 4.2. By our choice of L, $|v_i| < L$ along the orbit. The n-component of the orbit cannot hit the $n = K^\pm$ faces of $\partial\hat{N}$. (For example, if n has a local maximum at $z = 0$ and $n(0) = K^+$, then the last equation of (16) is contradicted.) If Y hits the boundary $p = 0$ or $p = 1$ of N_0, then $v_1 = 0$ also since Y lies in N_0. According to Lemma 4.4, $Y \equiv Y_3^\lambda$ or Y_1^λ which are in the interior of $\hat{N}$ because of the added neighborhood. Finally, if Y hits the boundary $v_1 = 0$ of N_0 and $p \neq 0$ or 1, then Lemma 4.4 implies that $Y \equiv Y^*$. Hence our assertion at the beginning of the paragraph is proved. We record it as a lemma.

LEMMA 4.5. *If $\theta \geq \theta_0 > 0$, then the only orbit of (16) in $I(\hat{N})$ which hits the boundary of $\hat{N}$ is $Y \equiv Y^*$.*

Finally, we must remove a neighborhood of Y^*. To do this, we use a result of [5] concerning the excision of a portion of an invariant set. Let S be a compact invariant set of a flow and $S_r \subset S$ an isolated set relative to S; that is, there is a compact relative neighborhood N_r of S_r in S such that $S_r = I(N_r)$. Let $A^+ = A^+(S, S_r)$ be the points on solutions in $S \backslash S_r$ that tend to S_r in forward time. Similarly, let $A^- = A^-(S, S_r)$ be those points which tend to S_r in backward time. A proof of the following lemma can be found in §4D of [5].

LEMMA 4.6. *Suppose $\tilde{N}$ is compact and $S = I(\tilde{N})$. Let $S_r \subset S$ be isolated relative to S and suppose that at least one of the sets A^+ and A^- is empty. Then for all sufficiently small neighborhoods W of S_r in $\tilde{N}$,*

$$(18) \qquad I(\tilde{N} \backslash W) \cap \partial(\tilde{N} \backslash W) = I(\tilde{N}) \cap \partial\tilde{N} \backslash (S_r \cup A^+ \cup A^-).$$

We will take $\tilde{N}$ to be $\hat{N}$ and S_r the rest point Y^*. In this case, $A^+(I(\hat{N}), Y^*)$ is the component of the stable manifold at Y^* that is contained in $I(\hat{N})$.

LEMMA 4.7. *For all* $\lambda \in [0,1]$ *and* $\theta > 0$, $A^+(I(\hat{N}), Y^*) = \emptyset$.

Proof. First note that if Y is a nonconstant orbit in $I(\hat{N})$, then by Lemma 4.2, $p \in [0,1]$ and by Lemma 4.4, $v_1 > 0$ for all z. Thus the only orbit in A^+ must be a heteroclinic connection from Y_3^λ to Y^*. For $\theta > 0$, there can be no such connection. The proof of this fact uses the same argument as in the second half of the proof of Lemma 4.4 and is omitted. Thus $A^+ = \emptyset$. □

The set $A^-(I(\hat{N}), Y^*)$ is nonempty since it is possible to find a connecting orbit, as for example when $\lambda = 0$, from Y^* to K_1^λ for sufficiently large θ. The unstable manifold at Y^* has dimension three and connecting orbits may be found using a shooting argument.

By Lemmas 4.6 and 4.7, for all sufficiently small neighborhoods W of Y^*, we have (18) holding. Since the λ-interval is compact, we can choose a neighborhood W so that (18) holds for all $\lambda \in [0,1]$. Finally, let $N = \hat{N} \backslash W$.

PROPOSITION 4.8. *N is an isolating neighborhood for the flow* (16) *for each* $\lambda \in [0,1]$ *and* $\theta \geq \theta_0 > 0$.

Proof. We must show that $I(N)$ is in the interior of N. From (18) and Lemma 4.7, we have

$$I(N) \cap \partial N = I(\hat{N}) \cap \partial \hat{N} \backslash (Y^* \cup A^-).$$

Suppose P belongs to $I(\hat{N}) \cap \partial \hat{N}$. If an orbit in $I(\hat{N})$ hits P in finite time, then by Lemma 4.5, $P = Y^*$. If P is approached by a nonconstant orbit Y in $I(\hat{N})$, then by Lemma 4.4 and the fact that the n-component of Y cannot have a local maximum (minimum) above (below) $g^\lambda = 0$, Y must connect two of the three rest points Y^*, Y_3^λ and Y_1^λ. It cannot connect Y_3^λ to Y^* because of Lemma 4.7. It cannot connect Y_3^λ and Y_1^λ since neither points are on $\partial \hat{N}$. Hence it must connect Y^* to Y_1^λ in which case $P = Y^*$. Finally, we have to consider the case when there exist orbits Y_n in $I(\hat{N})$ such that $Y_n(z_n) \to P$ as $n \to \infty$. Let $\hat{Y}_n(z) = Y_n(z_n - z)$. Then $\hat{Y}_n$ belongs to $I(\hat{N})$ and $\hat{Y}_n(0) \to P$ as $n \to \infty$. By the Arzela–Ascoli theorem, a subsequence of $\hat{Y}_n$ converges to an orbit $\hat{Y}$ in $I(\hat{N})$ where $\hat{Y}(0) = P$. From above, $P = Y^*$. Therefore, $I(N) \cap \partial N = \emptyset$ which completes the proof of the proposition. □

4.3. The proof of Theorem 2.1. We first derive a priori bounds on the wave speed θ.

LEMMA 4.9. *There exist* $0 < \theta_* < \theta^*$, *independent of* $\lambda \in [0,1]$, *such that if* $(\hat{p}, \hat{n})$ *is a nonconstant solution of* (13) *for some* θ *with* $\hat{p} \in [0,1]$, $\hat{p}' > 0$, $\hat{n} \in [n^*, K^+]$, $\limsup_{z \to -\infty} \hat{p}(z) < p_1^*$ *and* $\liminf_{z \to \infty} \hat{p}(z) > p^*$, *then* $\theta \in (\theta_*, \theta^*)$. *Here,* p_1^* *is the root of the equation* $f(p, K^+) = 0$ *that lies between zero and* 1.

Proof. We first show how to obtain the upper bound θ^* assuming that the lower bound θ_* has been found. Recall from the beginning of §4.2 that $\theta \geq \theta_*$ implies that $|\hat{n}'|$ is bounded independently of λ. Since $\hat{n} \geq n^*$, we can choose L_1 such that $|\hat{n}'/\hat{n}| \leq L_1$ for all z.

Consider the equation $w_t = w_{xx} + f^\lambda(w, K^+) w(1-w)$. Since

$$\int_0^1 f^\lambda(w, K^+) w(1-w) dw > 0,$$

this equation has a monotone travelling wave solution W^λ with positive wave speed

$\theta^{*,\lambda}$ such that $W^\lambda(-\infty) = 0$ and $W^\lambda(\infty) = 1$. Furthermore,

$$\theta^{*,\lambda} \int_{\mathbf{R}} ([W^\lambda]')^2 dz = \int_0^1 f^\lambda(w, K^+) w(1-w) dw.$$

This relation implies that $\theta^{*,\lambda}$ depends continuously on λ since $[W^\lambda]'$ depends on λ uniformly on $\mathbf{R}$. The travelling wave solution W^λ also has strong stability properties. Fife and McLeod showed in [10] that if the initial data w_0 satisfies the conditions $\limsup_{x\to-\infty} w_0(x) < p_1^*$ and $\liminf_{x\to\infty} w_0(x) > p_1^*$, then $w(x-\theta^{*,\lambda}t, t)$ is essentially bounded between two translates of W^λ.

Let $u(x,t) = \hat{p}(x+\hat{\theta}t)$ and $v(x,t) = \hat{n}(x+\hat{\theta}t)$ where $\hat{\theta} = \theta - 2\lambda L_1$. From (13), $\hat{p}'' - \hat{\theta}\hat{p}' + f^\lambda(\hat{p},\hat{n})\hat{p}(1-\hat{p}) \geq 0$ so that u satisfies the inequality $u_t \leq u_{xx} + f^\lambda(u,v)u(1-u)$. Since $f_n > 0$ and $n \leq K^+$, we have $u_t \leq u_{xx} + f^\lambda(u, K^+)u(1-u)$. Let w satisfy $w_t = w_{xx} + f^\lambda(w, K^+)w(1-w)$ with initial data $w_0 = \hat{p}$. From the maximum principle, $u(x,t) = \hat{p}(x+\hat{\theta}t) \leq w(x,t)$ for all x and $t > 0$. From the stability properties of W^λ mentioned above and our hypotheses on $\hat{p}$, there exist positive constants C, μ, and α such that

$$w(x - \theta^{*,\lambda}t, t) \leq W^\lambda(x-\alpha) + Ce^{-\mu t}$$

for all x and $t \geq 0$. Letting $y = x + (\hat{\theta} - \theta^{*,\lambda})t$, we have

$$\hat{p}(y) \leq W^\lambda(y + (\theta^{*,\lambda} - \hat{\theta})t - \alpha) + Ce^{-\mu t}.$$

If $\hat{\theta} > \theta^{*,\lambda}$, then letting $t \to \infty$ in the above inequality we obtain $\hat{p}(y) \leq 0$ for all $y \in \mathbf{R}$, which contradicts our hypotheses. Thus $\hat{\theta} \leq \theta^{*,\lambda}$. If we choose θ^* to be larger than $\max_{\lambda\in[0,1]}(\theta^{*,\lambda}) + 2L_1$, we obtain an upper bound for θ for all $\lambda \in [0,1]$. We now turn to finding θ_*.

Let $u = \hat{n}'/n$ and let $-\hat{\theta} = \min_z(-\theta + 2\lambda u(z))$. From the definition of f^λ, assumption (A4), and the hypotheses of our lemma, we have

$$\hat{p}'' - \hat{\theta}\hat{p}' + \beta(\hat{p} - p^*)\hat{p}(1-\hat{p}) \leq 0$$

where $\beta = 1 - \lambda + \lambda\alpha \geq \min(1,\alpha)$. This inequality implies that $\hat{\theta} = \theta - 2\lambda \min_z u(z) \geq \theta_*^\lambda$ where θ_*^λ is the wave speed of the bistable equation $w_t = w_{xx} + \beta(w-p^*)w(1-w)$. This fact may be proved using the same method we used to prove the upper bound θ^*. It is also known [2] that for the above bistable equation, θ_*^λ is given by $\sqrt{2\beta}(\frac{1}{2} - p^*)$. We now proceed to find the minimum of u.

If $n' \geq 0$, then $\min_z u(z) \geq 0$ so that $\theta \geq \sqrt{2\beta}(\frac{1}{2} - p^*) \geq \sqrt{2\min(1,\alpha)}(\frac{1}{2} - p^*)$. Suppose u is not monotone. Then u cannot have a local maximum. For if u achieves a local maximum at, say, $z = 0$, then $(\hat{p},\hat{n})(0)$ lies below $g^\lambda = 0$. Since $\hat{n}$ cannot have a local minimum below $g^\lambda = 0$, $\hat{n}$ is either increasing for $z < 0$ or decreasing for $z > 0$. But then this would imply that either $(\hat{p},\hat{n})(-\infty) = (0, K_3^\lambda)$ or $(\hat{p},\hat{n})(\infty) = (1, K_1^\lambda)$ which is impossible. Therefore, we assume that $\hat{n}$ has a unique minimum at $z = 0$, is decreasing on $(-\infty, 0)$, is increasing on $(0,\infty)$ and the minimum of u occurs at some point $z_0 < 0$.

From (13), u satisfies the equation $u' = -u^2 + \theta u - g^\lambda$ where $g^\lambda(z) = g^\lambda(\hat{p},\hat{n})(z)$. Therefore, $u(z_0) = (\theta - \sqrt{\theta^2 - 4g^\lambda(z_0)})/2$. Substituting this into the inequality $\theta - 2\lambda \min_z u(z) \geq \theta_*^\lambda$, we obtain

$$(1-\lambda)\theta + \lambda\sqrt{\theta^2 - 4g^\lambda(z_0)} \geq \sqrt{2\beta}\left(\tfrac{1}{2} - p^*\right).$$

To estimate $g^\lambda(z_0)$, we claim that if $(p_i, n_j), i, j = 1, 2$, are four corners of a rectangle in the p-n plane where $0 < p_1 < p_2 < 1$ and $0 < n_1 < n_2 < K_3^\lambda$, then $g^\lambda(p_1, n_1) + g^\lambda(p_2, n_2) \geq g^\lambda(p_1, n_2) + g^\lambda(p_2, n_1)$. Assuming this for the moment, let $(p_2, n_2) = (\hat{p}, \hat{n})(z_0)$ and $(p_1, n_1) = (0, n^*)$. Then $g^\lambda(z_0) \geq -\lambda g(0, n^*)$ which according to (7) is greater than $-(\epsilon^2 \min(1, \alpha))(\frac{1}{2} - p^*)^2/2$ for some $0 < \epsilon < 1$. Therefore, by completing the square and rearranging the last inequality of the last paragraph, we have $\theta \geq \sqrt{2}\min(1, \alpha)(1 - \epsilon)(\frac{1}{2} - p^*) \equiv \theta_*$.

To prove our claim, let $(\tilde{p}(z), \tilde{n}(z)), 0 \leq z \leq 1$ be a line segment joining the points (p_1, n_2) to (p_2, n_1) so that $\tilde{p}' \geq 0$ and $\tilde{n}' \leq 0$. Then, since $g_{pn}^\lambda = 2\lambda f_n \geq 0$, we have,

$$g^\lambda(p_2, n_1) = g^\lambda(p_1, n_2) + \int_0^1 g^\lambda(\tilde{p}(z), \tilde{n}(z))_z dz$$

$$= g^\lambda(p_1, n_2) + \int_0^1 (g_p^\lambda \tilde{p}' + g_n^\lambda \tilde{n}') dz \tag{19}$$

$$\geq g^\lambda(p_1, n_2) + \int_0^1 g^\lambda(\tilde{p}(z), n_1)_z dz + \int_0^1 g^\lambda(p_2, \tilde{n}(z))_z dz, \tag{20}$$

which is the same as our claim. The proof of the lemma is complete. □

We are now ready to apply the connection index theory to prove Theorem 2.1. Let $X = \mathbf{R}^4 \times [\theta_*, \theta^*]$ and $Y = X \times [0, 1]$ with the obvious flow Φ defined on Y. Let N be the set defined near the end of §4.2 with $\theta_0 = \theta_*$. Then Proposition 4.8 implies that $\hat{N} = N \times [\theta_*, \theta^*] \times [0, 1]$ is an isolating neighborhood for the flow Φ. Let $S' = Y_3^\lambda \times [\theta_*, \theta^*] \times [0, 1]$, $S'' = Y_1^\lambda \times [\theta_*, \theta^*] \times [0, 1]$ and $S = I(\hat{N})$. Then S, S', S'' are isolated invariant sets for the flow Φ on Y. We claim that for each λ, $(S(\lambda), S'(\lambda), S''(\lambda))$ is a connection triple. Conditions (i) and (ii) of Definition 2 are obvious and condition (iii) follows from Lemma 4.9 above. According to §3.2, the connection index $\bar{h}(\lambda) = \bar{h}(S(\lambda), S'(\lambda), S''(\lambda))$ is independent of λ. Hence, $\bar{h}(1) = \bar{h}(0)$. When $\lambda = 0$, (16) uncouples and $(n, v_2) = (n^*, 0)$ is a saddle point for the two-dimensional flow obtained by writing (15) as a first-order system. From the example given in §3.2, $\bar{h}(0) = \Sigma^1 \wedge \bar{0} = \bar{0}$. Therefore, $\bar{h}(1) = \bar{0}$.

To compute the Conley index $h(S'(1))$, we first observe that $S'(0)$ and $S'(1)$ are related by continuation. When $\lambda = 0$, $Y_3^0 = (0, 0, n^*, 0)$ and $Y_1^0 = (1, 0, n^*, 0)$. If we write (14) as a first-order system, then $(p, v_1) = (0, 0)$ and $(1, 0)$ are both saddle points. Each has a one-dimensional unstable manifold. Hence $h(S'(1)) = h(S'(0)) = \Sigma^1 \times \Sigma^1 = \Sigma^2$, according to §3.1. Similarly, $h(S''(1)) = \Sigma^2$. Since $(\Sigma^1 \wedge h(S')) \vee h(S'') = \Sigma^3 \vee \Sigma^2 \neq \bar{0} = \bar{h}(\lambda)$, Theorem 3.1 implies that there exists θ such that $I(N_\theta)$ contains a nonconstant orbit. From Lemma 4.4, this orbit must be a travelling wave solution connecting Y_3^1 to Y_1^1 with speed $\theta \in (\theta_*, \theta^*)$. Furthermore, p is increasing. Using the fact that n cannot have a maximum above the curve $g = 0$ or a minimum below the curve $g = 0$, it is easy to see that n can have at most one minimum on $\mathbf{R}$. The proof of Theorem 2.1 is complete.

5. A numerical example. In the previous section we showed how the homotopy invariance of the connection index allowed us to ascertain the existence of a travelling wave solution for the model (5). In this section we shall show that one can follow this heteroclinic connection for a specific example using numerical continuation techniques.

Recall from the introduction that

$$f(p, n) = p(\eta_1 - \eta_2) + (1 - p)(\eta_1 - \eta_3)$$

and

$$g(p,n) = p^2\eta_1 + 2p(1-p)\eta_2 + (1-p)^2\eta_3.$$

Following [13] we assume that the fitness functions have the form:

$$\eta_i(n) = r_i(1 - n/K_i) \quad \text{for } i = 1, 2, \text{ and } 3.$$

To obtain an example of the heterozygote inferior case we use the following values of parameters:

i	1	2	3
r_i	0.6	0.7	0.8
K_i	12000	7300	8000

For the numerical computations we have found it convenient to scale n by 10^3. It is easily checked that this corresponds to scaling the K_i's by 10^{-3} in the above table. Since g is linear in n and quadratic in p one can write down explicit formula for p^* and n^*. Furthermore, it is easy to check that assumptions (A1)–(A4) are satisfied for this model with the parameters given above.

We seek a heteroclinic orbit for (16) connecting Y_3^λ at $z = -\infty$ to Y_1^λ at $z = +\infty$, where $Y_3^\lambda = (0, 0, K_3^\lambda, 0)$, $Y_1^\lambda = (1, 0, K_1^\lambda, 0)$, and

$$K_i^\lambda = K_i \frac{(1-\lambda)n^* - \lambda r_i}{(1-\lambda)K_i - \lambda r_i} \quad \text{for } i = 1 \text{ and } 3.$$

It is easy to show that for each $\theta > 0$, (16) has a two-dimensional unstable manifold and a two-dimensional stable manifold at Y_i^λ for $i = 1$ and 3. One can also write down explicit expressions for the eigenvalues as well as a set of orthonormal eigenvectors. Let $\{\phi_3^\lambda, \psi_3^\lambda\}$ denote an orthonormal bases for the tangent space to the unstable manifold at Y_3^λ and $\{\phi_1^\lambda, \psi_1^\lambda\}$ an orthonormal bases for the tangent space of the stable manifold at Y_1^λ.

The numerical method used here is similar to the method given in [7]. The approximation is based on the following equations:

$$Y' = TF^\lambda(Y, \theta) \quad \text{for } 0 < z < 1, \tag{21}$$

with the boundary conditions:

$$Y(0) = Y_3^\lambda + \epsilon_3(m_{11}\phi_3^\lambda + m_{12}\psi_3^\lambda) \quad \text{with } m_{11}^2 + m_{12}^2 = 1, \tag{22}$$

and

$$Y(1) = Y_1^\lambda + \epsilon_1(m_{21}\phi_1^\lambda + m_{22}\psi_1^\lambda) \quad \text{with } m_{21}^2 + m_{22}^2 = 1. \tag{23}$$

Here, $F^\lambda(Y, \theta)$ is the vector field on the right-hand side of (16) and T is a large positive constant.

Equation (21) is just the differential equation (16) with z scaled by T. The boundary condition (22) is the requirement that the initial value $Y(0)$ lies on the sphere of radius ϵ_3 intersect the linear approximation to the unstable manifold at

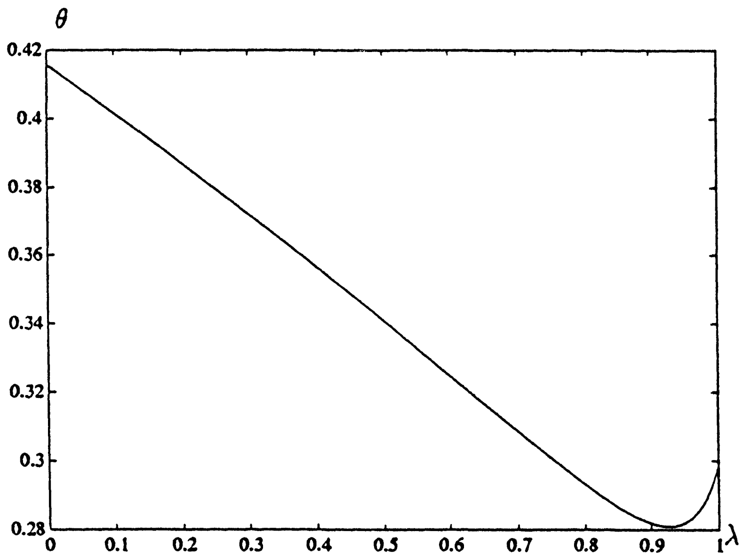

FIG. 5. *The wave speed θ versus the homotopy parameter λ.*

Y_3^{λ}. Likewise, (23) implies that $Y(1)$ lies on the sphere of radius ϵ_1 intersect the linear approximation to the stable manifold of Y_1^{λ}. The constant T is the time of travel between these two points for the original unscaled variable z. The m_{ij}'s are the projections onto the unstable and stable directions. For T large and ϵ_i's small, each solution of (20)–(22) represents an approximate heteroclinic connection.

In [7], the parameter T is fixed and the ϵ_i's are allowed to vary. Since the translate of a travelling wave is also a travelling wave, another constraint is needed to fix the phase of the solution. In [7], it was required that the L^2-norm of the difference between the derivatives of two successive approximations be at a minimum. This requirement takes the form of an integral condition. In the presence of sharp fronts, which occur for singularly perturbed equations, this condition is derived so as to economize the numerical calculations. For this model it is more economical to simply set $\epsilon_1 = \epsilon_3 \equiv \epsilon$, a fixed positive number, forego the integral constraint and allow T to be a free parameter. Along the solution branch we need to compute for each λ the solution vector Y, the wave speed θ, T and the m_{ij}'s so that the boundary conditions (21)–(22) hold.

To find a starting solution of (21) at $\lambda = 0$ we use $Y(z) = (u(z), u'(z), n^*, 0)$ where

$$u(z) = \frac{\exp(T\sqrt{2}/2(z-1/2))}{1+\exp(T\sqrt{2}/2(z-1/2))},$$

with $\theta = \sqrt{2}(1/2 - p^*)$. This is a solution of (16) at $\lambda = 0$ connecting Y_3^0 to Y_1^0. At $\lambda = 0$ we fix $T = 50$ and compute ϵ from the exact solution, thereafter holding ϵ fixed and allow T to vary. The numerical continuation is computed using the continuation program AUTO [8]. The results of this computation are shown below.

In Fig. 5 we have plotted the wave speed θ versus the homotopy parameter λ. In

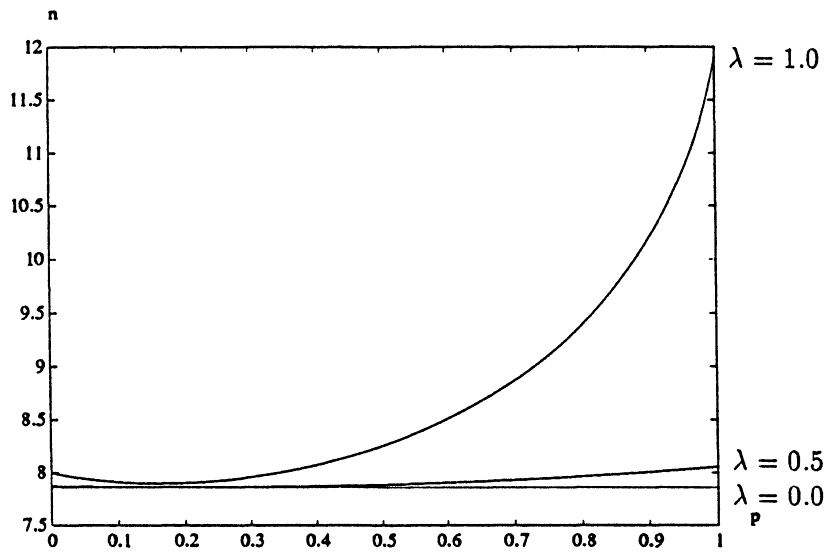

FIG. 6. *The n-component of the solution for* $\lambda = 0.0$, 0.5, *and* 1.0.

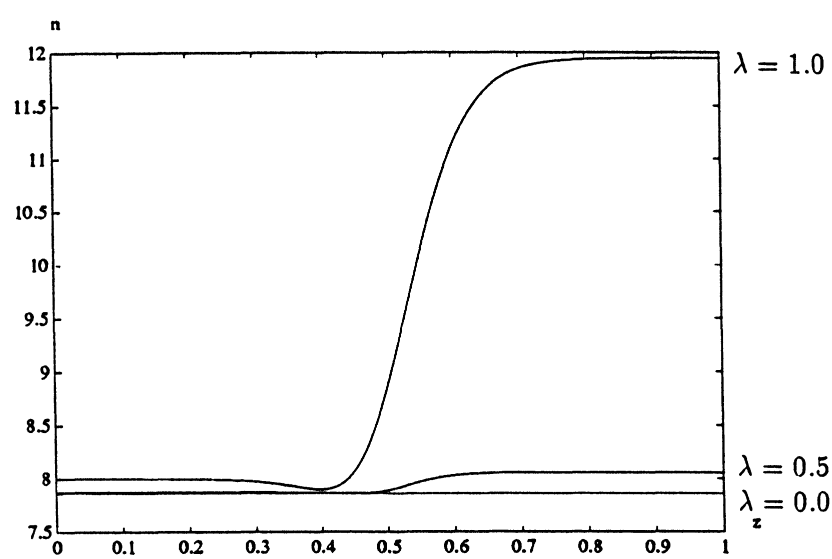

FIG. 7. *The projection onto the p-n plane of the solution for* $\lambda = 0.0$, 0.5, *and* 1.0.

Fig. 6 we have plotted the n-component of the solution as a function of z for $\lambda = 0, \frac{1}{2}$, and 1. We see that n is clearly not monotone at $\lambda = 1$. In Fig. 7 we have plotted the projection of the solutions for $\lambda = 0, \frac{1}{2}$, and 1 onto the p-n phase plane.

Acknowledgment. Part of this work was performed while the first author was visiting the Institute for Applied Mathematics and Its Applications and the second author was visiting the University of Utah. Both authors are indebted to their host institutions for their support.

REFERENCES

[1] D. G. Aronson and H. F. Weinberger, *Nonlinear diffusion in population genetics, combustion and nerve propagation*, in Partial Differential Equations and Related Topics, J. Goldstein, ed., Lecture Notes in Math. 446, Springer-Verlag, Berlin, New York, 1975, pp. 5–49.

[2] R. Casten, H. Cohen, and P. Lagerstrom, *Perturbation analysis of an approximation to the Hodgkin–Huxley theory*, Quart. Appl. Math., 32 (1975), pp. 365–402.

[3] C. Conley, *Isolated invariant sets and the Morse index*, AMS Reg. Conf. Ser. Math., Vol. 38, American Mathematical Society, Providence, RI, 1978.

[4] C. Conley and J. Smoller, *Isolated invariant sets of parameterized systems of differential equations*, in The Structure of Dynamical Systems, N. G. Markley, J. C. Martin, and W. Perrizo, eds., Lecture Notes in Math. 668, Springer-Verlag, Berlin, 1978.

[5] C. Conley and R. Gardner, *An application of the generalized Morse index to travelling wave solution of a competitive reaction–diffusion model*, Indiana Univ. Math. J., 33 (1984), pp. 319–343.

[6] J. Crow and M. Kimura, *An Introduction to Population Genetics Theory*, Burgess, Minneapolis, MN, 1970.

[7] E. J. Doedel and M. J. Friedman, *Numerical computation of heteroclinic orbits*, J. Comput. and Appl. Math., 26 (1989), pp. 159–170.

[8] E. J. Doedel and J. P. Kerevez, AUTO: *Software for continuation and bifurcation problems in ordinary differential equation*, Applied Mathematics Report, California Institute of Technology, Pasadena, CA, 1986.

[9] P. C. Fife, *Mathematical Aspects of Reacting and Diffusing Systems*, Lecture Notes in Biomath. 28, Springer-Verlag, Berlin, New York, 1979.

[10] P. C. Fife and J. B. McLeod, *The approach of solutions of nonlinear diffusion equations to travelling front solutions*, Arch. Rational Mech. Anal., 65 (1977), pp. 335–361.

[11] R. A. Fisher, *The advance of advantageous genes*, Ann. Eugenics, 7 (1937), pp. 355–369.

[12] R. Gardner, *Existence of travelling wave solutions of predator-prey systems via the connection index*, SIAM J. Appl. Math., 44 (1984), pp. 56–79.

[13] J. Roughgarden, *Density-dependent natural selection*, Ecology, 52 (1971), pp. 453–468.